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DOI: https://doi.org/10.1080/03736687.2018.1551829

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Keywords. Britain, China, Himalayas, *Hygrohypnum eugyrium, Hygrohypnum luridum, Hygrohypnum subeugyrium*, India, *Pseudohygrohypnum*, Sikkim, Yunnan.

Introduction

Hygrohypnum subeugyrium was first described by Renauld & Cardot (1896) from Newfoundland as *Hypnum subeugyrium*. In the protologue the new species was compared with *Hypnum eugyrium* (Schimp.) Sull. var. *mackayi* Schimp. (*Hygrohypnum eugyrium* (Schimp.) Loeske var. *mackayi* (Schimp.) Broth.), and it was said to differ in the alar cells of the leaves being small, quadrate and not forming excavate auricles, and in the exannulate capsules. It was subsequently recognised in many American Floras (e.g. Grout, 1931; Crum & Anderson, 1981; Jamieson, 2014; Allen, 2014; Faubert, 2014). However, although Grout mentioned a report from Europe (Sweden) by Carl Stenholm, its presence in Europe received little attention in the 20th century and it was not included in the Floras of Jensen (1939) and Nyholm (1965).

For his doctoral thesis at the University of British Columbia, Jamieson (1976) wrote a monographic revision of the genus *Hygrohypnum* as then defined, recognising 16 species in the genus. His revision was the basis for the account of *Hygrohypnum* in the *Flora of North America* (Jamieson, 2014). In his monograph he maintained *H. subeugyrium* as a distinct species, and confirmed its occurrence in Sweden. He also reported a single specimen from Scotland (Loch Sunart, Argyll) collected in 1954 by E.C. Wallace and A.C. Crundwell. Corley & Crundwell (1991) noted the occurrence of the species in Sweden and Scotland, but Smith (2004) failed to mention it in the second edition of his *Moss Flora of Britain and Ireland*. Consequently it has been neglected as a British moss and has received little attention in Europe. The *Flora of Middle European Russia* (Ignatov & Ignatova, 2004) and the Swedish *Nationalnyckeln* series (Hedenäs & Hallingback, 2014) contain the only substantial accounts of the species in European Floras.

During a meeting of the British Bryological Society in 2017, the participants explored many parts of the Applecross Peninsula in West Ross (Long, 2018). The second author of the present paper (TK) collected material of *Hygrohypnum* that he subsequently identified as *H. subeugyrium*. The first author (TLB) agreed with this identification, and it was later confirmed by Lars Hedenäs (Swedish Museum of Natural History). Once this became known, other participants found that they had also collected the same species. A subsequent revision of herbarium material at the Royal Botanic Garden, Edinburgh (E) and at the National Museum of Wales, Cardiff (BBSUK, NMW) revealed that *H.*

subeugyrium occurs widely in western Scotland and extends southwards to a few localities in England and Wales.

Description of British plants

The following description is based on British material. Characters not available or observed in British plants but described by Jamieson (1976) are included in square brackets.

Hygrohypnum subeugyrium (Renauld & Cardot) Broth., *Nat. Pflanzenfam.* 231[I,3]: 1039, 1908 (Figures 1-2)

Plants in mats or loose patches, usually attached to rocks in and by streams. Shoots irregularly branched, typically 2-5 cm long, variously green to blackish-brown or black, the mature parts sometimes developing reddish or reddish-brown pigmentation. Stems with central strand weak or absent; stem cortex of small incrassate cells, the outermost row not differentiated from the inner rows. Axillary hairs with 2-5 upper cells, hyaline to pale yellow-green, the basal cell a little darker. Leaves to 1.75 mm long, ovate to ovate-elliptical, concave, often somewhat falcate or secund, weakly sheathing the stem at the base, gradually tapered to an acute, subacute or, more commonly, obtuse apex; margins plane, frequently with distinct denticulations at and just below the apex, otherwise entire, sometimes more or less entire throughout. Nerve usually double and short, branched at or near the base, occasionally unbranched (though often with a rudimentary lateral spur on one or both sides near the base) and reaching to around mid-leaf. Median leaf cells linear, mostly in the range 40-75 µm long. Alar groups variable, usually well-defined, normally wider than tall, the cells thick-walled, variously elongate or more or less shortly rectangular to irregularly isodiametric, or sometimes quadrate, the basalmost 1-2(-3) rows often forming a band of enlarged, strongly incrassate, bulging cells across the leaf base.

Autoicous. Perigonia bud-like, the leaves broadly ovate or ovate-oblong. Outer perichaetial leaves ovate-triangular to ovate-lanceolate with reflexed apices; inner perichaetial leaves erect, often very long (to 3.5 mm), lanceolate to linear-lanceolate, plicate, denticulate or not at the apex; nerve indistinct [sometimes elongate and single]. Seta erect, 1-2 cm long, smooth. Capsules asymmetrically obovoid-cylindrical, curved, to *ca* 2.5 mm long (excluding lid). [Annulus present.] Exothecial cells irregularly oval to elliptical-rectangular, with incrassate walls. Peristome double; exostome teeth 16, horizontally striate below, papillose above; endostome of 16 ± hyaline, finely papillose segments alternating with 1-2 cilia, which may be as long as the segments. Spores 12-20 µm, finely papillose. [Lid conical.]

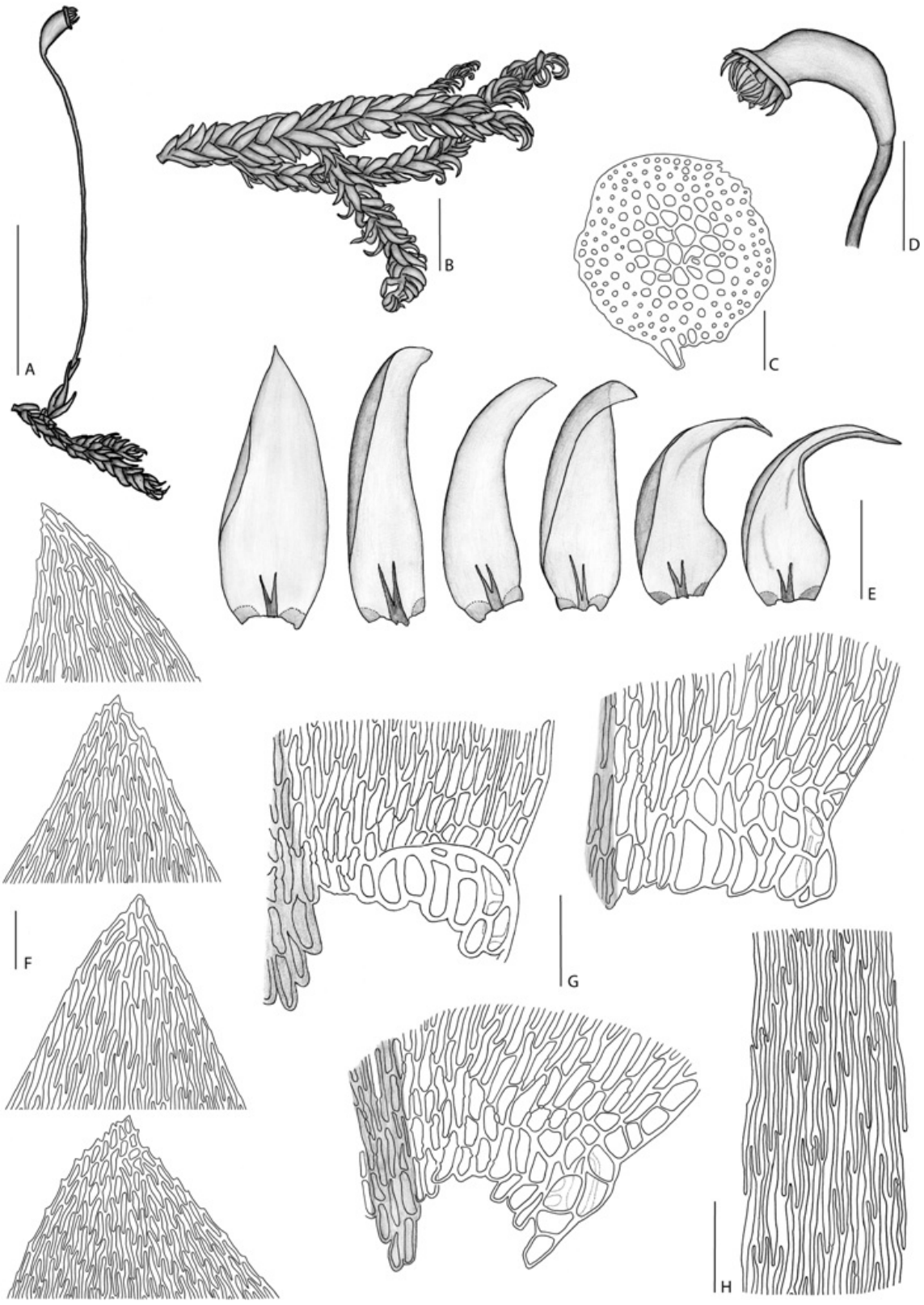

Fig. 1. *Hygrohypnum subeugyrium* (Renauld & Cardot) Broth. (A) Shoot with sporophyte, dry. (B) Habit of gametophyte, dry. (C) Stem cross section. (D) Capsule, dry. (E) Stem leaves, ventral view, wet. (F) Stem leaf apices. (G) Alar cells of stem leaves. (H) Mid-leaf cells of stem leaf. Scale bars: (A) = 5 mm; (B) = 2 mm; (C, F-H) = 50 µm; (D) = 1 mm; (E) 0.5 mm. All from *T. Kiebacher 1519*.

Differentiation

Hygrohypnum subeugyrium is characterised by: (1) ability to develop reddish pigmentation, (2) leaves concave, often somewhat falcate or secund, ovate or ovate-oblong, evenly tapered to an acute, sub-acute or commonly obtuse apex; (3) leaf apex often with distinct denticulations; (4) nerve usually double; (5) alar groups wider than tall, composed of thick-walled cells and often with a distinct band of 1-2(-3) rows of large bulging cells across the base; (6) outer cells of stem cortex small, similar in size to the subepidermal cells, evenly thick-walled. As in many other *Hygrohypnum* species the diagnostic characters (leaf shape, alar groups, development of the nerve) are quite variable, even on a single stem, and it is good practice to examine leaves from several shoots.

The reddish-brown pigmentation of *H. subeugyrium* is sometimes very distinctive, but is not always present. According to Allen (2014) the reddish colour extends to the axillary hairs, which are sometimes deep red, but we have not observed this in British material. Renauld & Cardot (1896) described the capsules of *H. subeugyrium* as exannulate. We have not seen young operculate capsules of this species, but according to Jamieson (1976) an annulus is in fact present in young capsules but is lost soon after dehiscence.

Most of the herbarium specimens of *H. subeugyrium* were originally labelled as *H. eugyrium* and this is the species with which it is most likely to be confused. Both species commonly have a double nerve and enlarged alar cells, and they occasionally develop reddish pigmentation, though only rarely in *H. eugyrium*. However, they differ in a number of morphological characters. The leaves of *H. eugyrium* are typically (but not always) more broadly ovate-elliptical than those of *H. subeugyrium*, and they contract rather abruptly to the apex, which often appears apiculate. This is exaggerated by the tendency of the leaf apex in *H. eugyrium* to be channelled with erect margins. The leaf apices are acute or sub-obtuse, and occasionally denticulate, but less often than in *H. subeugyrium*. The leaves of *H. subeugyrium* are, on average, more narrowly ovate or ovate-oblong, and more evenly tapered to the apex, which is often broadly obtuse, rarely appearing apiculate. The leaf bases of *H. eugyrium* are more strongly sheathing than those of *H. subeugyrium*, and the bases of dissected leaves can often be seen to have a semi-circular profile. As with many aquatic mosses, leaf shape in both species can be quite variable, and it is occasionally possible to find leaves of similar shape on shoots of the two species.

The morphology of the alar cells and the stem offer more reliable means of identification. The alar groups of *H. subeugyrium* are normally wider than tall, and they consist of thick-walled cells (Fig. 1G). Often there is a band of enlarged, strongly incrassate, bulging cells in 1-2(-3) rows across the base of the alar groups (Fig. 2A), and these cells are doubtless the reason why British specimens have been named *H. eugyrium* in the past. However, the alar groups of *H. subeugyrium* are rather variable and the band of bulging cells is sometimes poorly developed or absent. In such cases the alar groups consist of thick-walled cells that are scarcely inflated. In *H. eugyrium* the alar groups are isodiametric in shape and very clearly defined (Fig. 3A); in young leaves the constituent cells are inflated and hyaline; in mature leaves the inner cells develop thick, highly coloured walls, while the outermost 1-2 rows typically remain rather thin-walled and often collapse. The alar groups are separated from the nerve by thick-walled, porose, linear cells that are often coloured like the alar cells, and may give the impression that the alar groups extend across the leaf base. The shape of the alar groups and the presence of strongly inflated cells distinguish *H. eugyrium* from forms of *H.*

subeugyrium in which the basal band of bulging cells is not or weakly developed. When the band of bulging cells is present in *H. subeugyrium*, it is very distinctive, being wider than tall and clearly different from the isodiametric groups of *H. eugyrium* (Figs 2A, 3A).

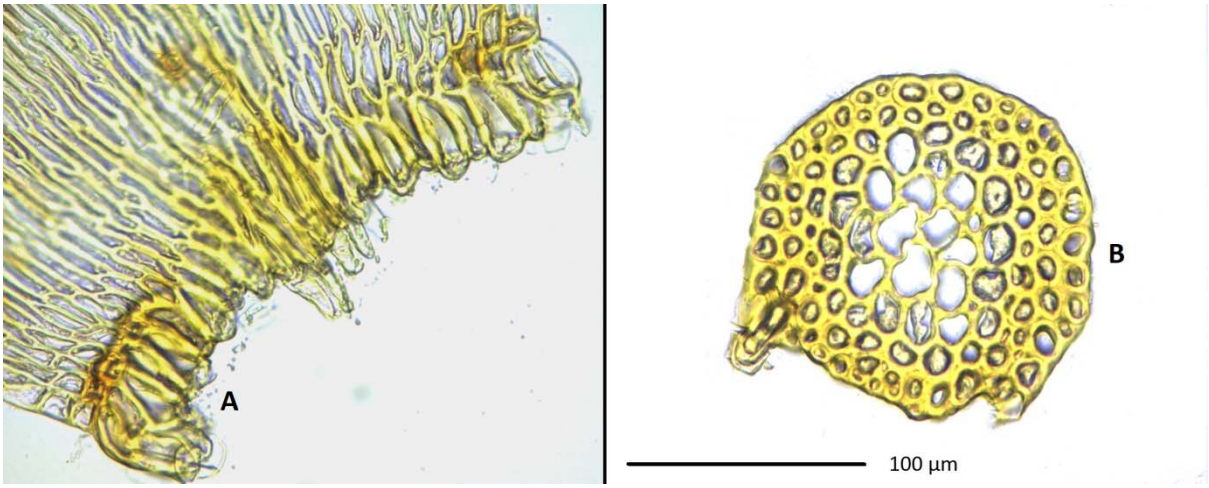

Fig.2 Leaf base and stem section of *Hygrohypnum subeugyrium*. (A) bulging row of alar cells, (B) stem cortex with thick-walled outer cells.

In the stems of *H. subeugyrium* the central strand is poorly developed or lacking, and the outermost row of the cortex consists of small evenly thick-walled cells with small lumens (Figs. 1C, 2B). In *H. eugyrium* the stem has a well-developed central strand and the cells of the outermost row of the cortex are slightly enlarged, with their outer walls thinner than the inner walls, and they have the appearance of a weak hyalodermis (Fig. 3B). Our observations suggest that this latter character is constant and reliable. However, care is needed when examining dried herbarium specimens as the outer walls of the cortex often collapse towards the inner walls (Fig 3C), resulting in a crenulate outline, and can lead to the false assumption that enlarged cells are absent.

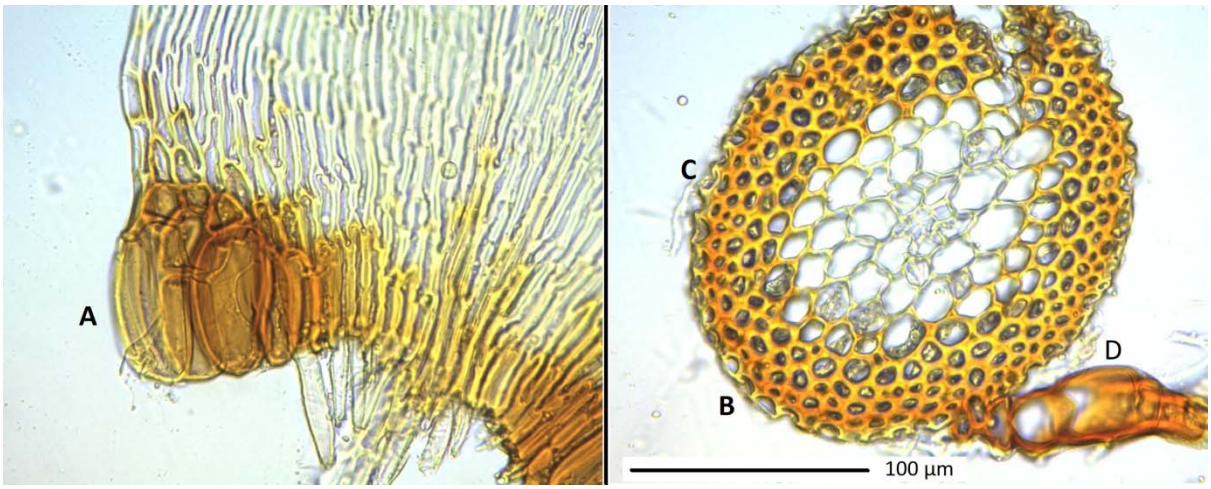

Fig.3 Leaf base and stem section of *Hygrohypnum eugyrium*. (A) isodiametric group of large inflated alar cells, (B) weakly differentiated stem cortex with thin outer walls, (C) stem cortex with outer walls tending to collapse inwards, (D) alar cells in section

A few herbarium specimens of *H. subeugyrium* were named *H. luridum* (Hedw.) Jenn. at the time of collection. This is hardly surprising: after the elimination of *H. eugyrium* and without knowledge of *H.*

subeugyrium, the default name for specimens of the latter would invariably be *H. luridum*. The two species are very similar in leaf shape, and the alar cells of *H. subeugyrium* can be rather similar to those of *H. luridum* if the band of enlarged cells at the leaf base is absent or poorly developed. In addition, the alar cells in some forms of *H. luridum* may be enlarged and somewhat excavate. However, *H. luridum* differs in the presence of a single nerve in the majority of leaves (occasionally the nerve is forked or double), and in the constant absence of distinct denticulations at the leaf apex. In all specimens of *H. subeugyrium* seen by us at least some leaves have distinctly denticulate apices.

Relationships of *H. subeugyrium*

Morphologically, *Hygrohypnum subeugyrium* has many similarities with *H. eugyrium*: leaves that are longer than wide, concave and frequently secund, leaf apices that may be denticulate, nerve usually double, enlarged alar cells, and the ability to develop reddish pigmentation. In his discussion of *H. subeugyrium* Jamieson (1976, p. 352) notes that "the relationship between the two taxa [*H. eugyrium* and *H. subeugyrium*] is a remote one and the choice of subeugyrium as a specific epithet mistakenly implies a closer relationship". On the other hand, he performed a cluster analysis based on 89 character states, and this clearly indicated a close similarity between the two species. In commenting on this analysis, Jamieson (p. 415) states that the two species "exhibit the highest degree of similarity between any two species in the genus". Further evidence for a close relationship between the two species was provided by Oliván *et al*. (2007) using molecular data. Previously Kanda (1976) had already transferred *H. eugyrium* and *H. purpurascens* Broth. (a synonym of *H. subeugyrium*) to a new genus *Pseudohygrohypnum* Kanda. The formal combination *Pseudohygrohypnum subeugyrium* was made by Ignatov & Ignatova (2004).

As traditionally defined, the genus *Hygrohypnum* is a heterogeneous group of species and molecular evidence shows that it is not monophyletic, and that the constituent species belong to different families of bryophyta (Vanderpoorten *et al.*, 2002; Gardiner *et al*., 2005; Oliván *et al*., 2007). Vanderpoorten *et al.* (2002) found that the Amblystegiaceae were polyphyletic and that *Hygrohypnum luridum* belonged in the Amblystegiaceae s.str. but *H. ochraceum* (Turner ex Wilson) Loeske in the Calliergonaceae. The molecular data of Gardiner *et al*. (2005) indicated that *Hygrohypnum eugyrium* belonged in the Pylaisiaceae (*H. subeugyrium* was not included in their sampling). In the analysis of Oliván *et al*. (2007) the species of *Hygrohypnum* were placed in four well-supported clades, one of which included the two species of *Pseudohygrohypnum* (their clade C). The other British species of the genus were distributed as follows:

Clade A. *H. styriacum* (Limpr.) Broth. and *H. luridum*

Clade B. *H. ochraceum* and *H. polare* (Lindb.) Loeske

Clade D. *H. duriusculum* (De Not.) D.W. Jamieson*, H. molle* (Hedw.) Loeske and *H. smithii* (Sw.) Broth.

H. styriacum and *H. luridum* belong to *Hygrohypnum* s.str., of which *H. luridum* is the type species. Even before the study of Oliván *et al*., Ignatov & Ignatova (2004) had already transferred *H. ochraceum* and *H. polare* to a new genus *Hygrohypnella* Ignatov & Ignatova, and *H. smithii* to the genus *Ochyraea* Váňa. The formal transfer of *H. duriusculum* and *H. molle* to *Ochyraea* soon followed (Ignatov *et al.*, 2006; Ignatov *et al.*, 2007). Thus, the British species potentially belong to four discrete genera. Oliván *et al*. (2007) noted that their results were not in complete agreement with earlier studies and they thought that "further nomenclatural changes would be premature at this

point" and that further sampling of *Hygrophypnum* and closely related taxa was required to confirm or establish a new classification of *Hygrohypnum*. However, the recent anlaysis of Câmara *et al*. (2018) provides further strong evidence for the placement of *Pseudohygrohypnum* (including *P. eugyrium* and *P. subeugyrium*) in the Pyliasiaceae.

Ecology and Distribution

Most British records of *Hygrohypnum subeugyrium* at the present time are based on herbarium specimens, and full details of its ecology are not yet known. It is primarily a moss of running water, typically in swift-flowing rocky streams. However, one of the English localities is on the margins of a lake, and a Scottish one is from muddy stones by a loch. It usually grows attached to rocks, but it has also been collected from the roots of an Ash tree (*Fraxinus excelsior*). Some sites are sheltered or shaded, for example in wooded ravines, but others are in the open. The Applecross Peninsula, where *H. subeygyrium* was found at four sites in 2017, is composed largely of acidic Torridonian Sandstone, and a preference for base-poor substrates seems to be characteristic of *H. subeugyrium*. It is not known from limestone. At some sites it is associated with *H. eugyrium*, and mixed gatherings of the two species are known. Most of the known sites are at low altitudes, below 250m a.s.l., but it ascends to 800m at Moy Corrie, Creag Meagaidh in Scotland.

Sporophytes are occasionally present in *H. subeugyrium*. Capsules mature in the summer, and on the basis of material seen by us are already quite old and empty in August-September.

Confirmed records of *H. subeugyrium* in Britain are listed in Appendix 1 and are mapped in Fig. 4. As the records are based largely on herbarium specimens, many of them are old but it is likely that most of the sites are still extant. The apparently oceanic distribution may simply be due to the prevalence of mountainous terrain in the north and west of Britain. On a worldwide basis *H. subeugyrium* is not an oceanic species, being incompletely circumpolar. In Europe it is known from southern Sweden (Hedenäs & Hallingback, 2014) and southern Norway (http://artskart.artsdatabanken.no/FaneArtSok.aspx). The only other report from Europe that we have traced is from the South Urals in Russia (Czernyadjeva, 2003). Outside Europe, Jamieson (1976) cites specimens from western North America (Canada and the United States, south to Tennessee) and from Eastern Asia (Japan and Korea). Since then it has been shown to be widespread in many of the territories of Russian Asia, *viz*. Arctic East Siberia, East Siberia, South Siberia, Yakutia, North Far East and South Far East (Czernyadjeva, 2003; Ignatov *et al*., 2006).

During expeditions to the Sino-Himalayan region, the third author of the present paper (DGL) along with J. Shevock has collected *H. subeugyrium* in Yunnan (China) and Sikkim (India), and we report it here as new for these territories. Full details of the records are given in Appendix 2. The habitats in the Himalayan region are similar to those in Britain, but of course at higher altitudes (2510-4090m). In Sikkim it was collected from wet dripping rocks in a cascade, and in Yunnan it occurred on rock slabs and boulders (frequently granitic) in and by streams.

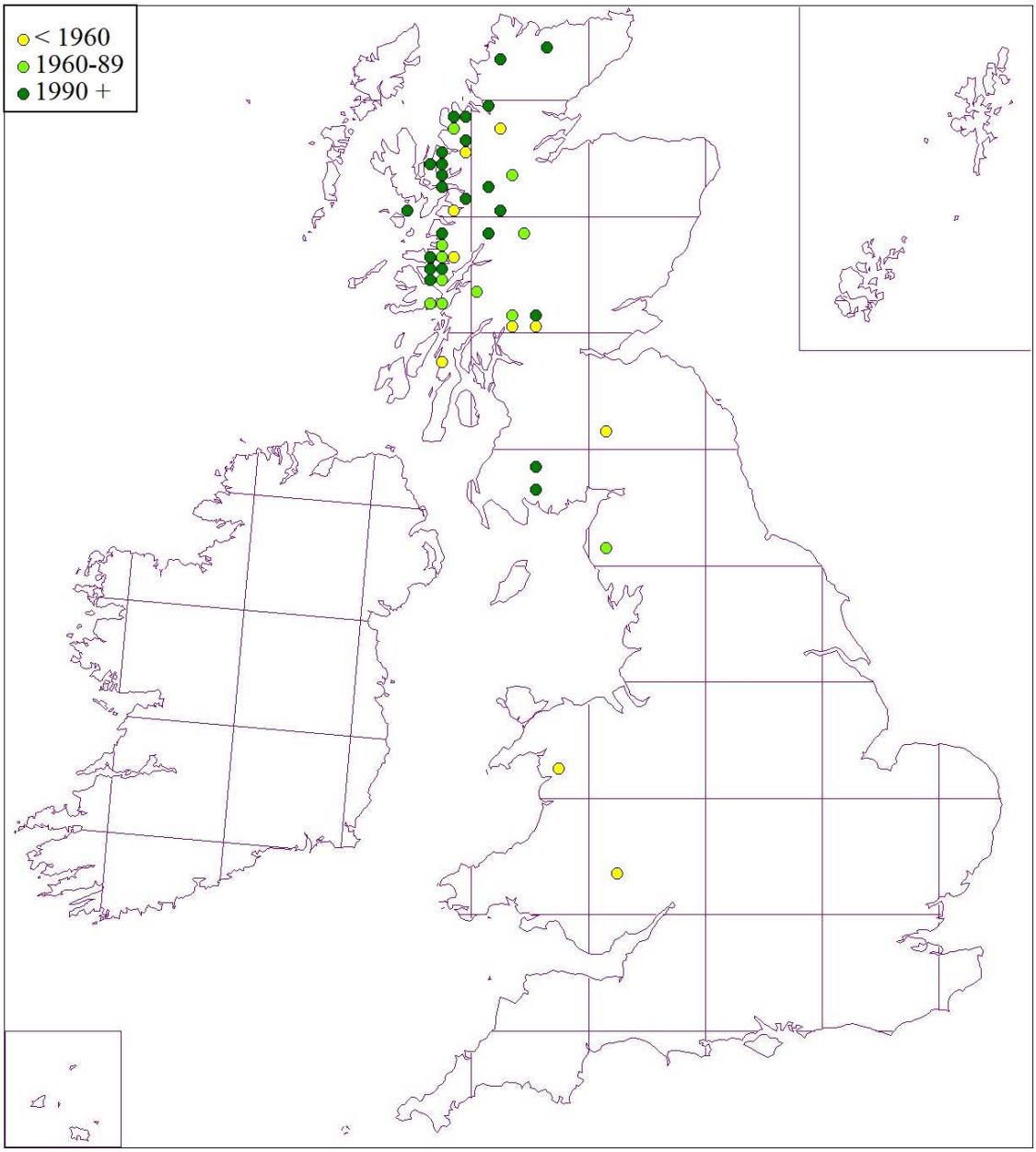

Fig. 4. Distribution of *Hygrohypnum subeugyrium* in Britain as currently known

Summary Comments

Many *Hygrohypnum* species exhibit wide variation in morphological characters, and are therefore difficult to circumscribe succinctly. In spite of this variation, *H. subeugyrium* emerges as species that is well-defined morphologically. We have had little difficulty in identifying the material that we have seen. Its neglect in Britain since the publication of Jamieson's (1976) thesis can be explained by its omission from the *Moss Flora of Britain and Ireland* (Smith, 2004) and the lack of adequate descriptions before Jamieson's thesis was made available on the internet. Unfortunately, the figure of the alar cells in Crum & Anderson (1981) was not very helpful, as it failed to show the enlarged, bulging cells that are often present in the species. With increased awareness, further records can be expected in Britain and it is likely to occur in Ireland, too.

Taxonomic Additions and Changes: Nil

Acknowledgments
We are very grateful to Lars Hedenäs for confirming the identity of specimens of *H. subeugyrium* from Scotland and the Himalaya, and to Liz Kungu for checking and forwarding a number of Scottish specimens. Jim Shevock, California Academy of Sciences, is thanked for his permission to cite his collections from China. The map in Figure 4 was prepared using Dr Alan Morton's DMAP for Windows, version 7.4b.

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Appendix 1. Confirmed records of *Hygrohypnum subeugyrium* in Britain

Records are grouped by vice-county ("v-c"), in accordance with the British Bryological Society's vice-county recording scheme (see Hill *et al*., 2008).

Herefordshire (v-c 36): head of Olchon Valley, Black Mountains, submerged on blocks in cascading stream, SO23, 5 April 1968, H.J.B. Birks & H.H. Birks (BBSUK: C.2001.019.16933).

Merioneth (v-c 48): road to Pistyll-y-Cain, near Dolgelley, SH72, August 1920, J.B. Duncan & W.N. Tetley (BBSUK: C.2001.019.5677).

Cumberland (v-c 70): Blackbeck, Haystacks, submeged on blocks in stream, NY1913, 19 September 1966, H.J.B. Birks s.n. (E: 00434355); The Side, S shore of Ennerdale Water, siliceous boulder in water, NY1213, 6 September 1973, A.R. Perry (NMW: 85.18.98); The Side, S shore of Ennerdale Water, roots of *Fraxinus* at edge of water, NY1213, 6 September 1973, A.R. Perry (NMW: 79.88B.88).

Dumfriesshire (v-c 72): small burn joining Tail Burn, Moffatdale, rocks in burn, NT11, August 1950, R. Hall (NMW: C.1999.030).

Kirkcudbrightshire (v-c 73): Moneypool Burn, upstream of Falbae Bridge, on rocks at the edge of the stream, 85m, NX5034161025, 14 September 2009, A. Bell (E); Glenlee Burn, S bank, on rocks at the edge of the stream, with *H. eugyrium*, 70m, NX599809, 20 August 2017, E.M. Kungu, V. Heppel & E.-J. Sadler (E).

West Perthshire (v-c 87): Ben Ledi, NN50, 29 July 1899, R.H. Meldrum s.n. (E: 00844502); Calair Burn above Ballimore, Glen Buckie, Balquidder, on boulder by water, wooded valley, 210m, NN52771736, 18 July 2017, D.G. Long 44870 (E).

Easterness (v-c 96): R. Affric, d/s Loch Affric, rocks in river, 230m, NH1987523272, 4 August 2015, J. McDonald & R. Watts (E); Ravine at Cannich, S side, on stones in river, 110m, NH334318, 29 July 1988, D.G. Long 15322 (E: 00844504).

Westerness (v-c 97): Glen Arnisdale, Loch Hourn, boulders in river, NG80, 1 June 1955, E..C. Wallace 3034 (E: 00844527); R. Garry, u/s of Whitebridge, rocks in river, with *Hygrohypnum ochraceum*, 70m, NH2806501547, 16 August 2017, J. McDonald & M. Nicolson (E); R. Garry, u/s of Aldernay Burn, rocks in river, with *Hygrohypnum ochraceum*, 45m, NH2977900871, 16 August 2017, J. McDonald & M. Nicolson (E); R. Aline, d/s A884 [south of Acharn], rocks in river, 10m, NM6967149460, 8 June 2016, M. Nicolson & R. Watts (E); Camas Glas, Loch Sunart, in ravine in wood, NM6458, 1 July 1954, E.C. Wallace & A.C. Crundwell s.n. (E: 00844511); Loch Doire nam Mart, Morvern, on boulder on loch margin, 10m, NM663524, 7 May 1998, G.P. Rothero 98032 (Herb. Rothero); Allt a Chamais Shalaich ravine, on boulder in shady ravine, 50m, NM684611, 28 July 1986, D.G. Long 13628 (E: 00844508); Allt a Chamais Shalaich, Loch Sunart, wooded ravine; on damp rocks by burn, 50m, NM685610, 23 May 2001, D.G. Long 29794 (E: 00844503); Stream above Achranich, Ardtornish, Morvern, wet shaded rocks in stream, 30m, NM7047, 9 July 1978, D.G. Long 7064 (E: 00844529); W side of lower Gleann Dubh, 7 km N of Lochaline, on rocks in rivulet, NM75, 6 July 1978, C.C. Townsend 78/460 (E: 00844515); Allt Coire Reidh, S side of Loch Sunart, rocks in ravine, NM7459, 1 June 1952, E.C. Wallace & A.C. Crundwell s.n. (E: 00844510); R. Aline, Acharn, rocks in river, 10m, NM7012050281, 8 June 2016, M. Nicolson & R. Watts (E); Allt Creag an Eighich, Camasine, Loch Sunart, NM76, 10 September 1970, E..C. Wallace s.n. (E: 00844526); Resipole ravine, Sunart, on boulder in stream in wooded ravine, 50m, NM7264, 28 May 1989, D.G. Long 16183 (E: 00844505); Kinlochmoidart, burn above Post Office, rock in burn, 200 ft., NM77, 14 April 1972, A.M. Ballantyne s.n. (E: 00844528); R Ailort at Glenshian Lodge, on rocks in river, 10m, NM7678382201, 21 June 2012, M. Nicolson & J. Forsyth (E); Ariundle, NM86, 6 September 1964, D.A. Ratcliffe s.n. (E: 00797156); R. Lochy, Carnisky, rocks in river, 40m, NN1412480201, 20 June 2012, M. Nicolson & J. Forsyth (E); Moy Corrie, Creag Meagaidh, on muddy stones by loch, 800m, NN435867, 24 July 1981, D.G. Long 9656 (E: 00844530).

Main Argyll (v-c 98): Bonawe, Loch Etive, rocks in stream, NN0033, 9 August 1971, M.F.V. Corley s.n. (E: 00844514).

Dunbartonshire (v-c 99): Loin Burn, Arrochar, NN30, April 1915, J.C. Adam s.n. (E: 00844525); Stuckgowan Burn, NN3202, 1 May 1965, A.McG. Stirling s.n. (E: 00242007); south of Inveruglas, lochside, NN30, 26 November 1960, I.D. Clear (NMW: C93.19.1781); Stuckindroin ravine, Ardlui, rocks in stream in ravine woodland, 50m, NN3114, 26 November 1987, N.G. Hodgetts (E).

Kintyre (v-c 101): Allt Cinn-locha, Lochead, Loch Caolisport, wet rocks in stream, NR7778, 29 August 1967, M.F.V. Corley s.n. (E: 00844513); Allt Cinn-locha, Lochead, Loch Caolisport, wet rocks in stream, NR77, 29 August 1967, M.F.V. Corley (BBSUK: C2001.019.16941).

Mid Ebudes (v-c 103): Allt a'Bhaird, S of Lochbuie, Mull, wet rocks at edge of stream in ravine, NM6323, 16 September 1981, M.F.V. Corley s.n. (E: 00844509); Croggan, S side of Loch Spelve, Mull, wet rocks in stream in wood, NM7027, 18 September 1982, M.F.V. Corley s.n. (E: 00844531).

North Ebudes (v-c 104): Rum, between Camas Pliasgaig and Creag na h-Iolaire, wet rock below small fall in burn, 50m, NG40200213, 28 June 2004, G.P. Rothero 14164 (Herb. Rothero); Mudalach, Skye, on rock in coastal burn, NG72S, 2017, S.D.S. Bosanquet (BBSUK).

West Ross (v-c 105): Allt Tasabhaig, Applecross, rock in river, NG68524806, 28 July 2017, P. Martin s.n. (hb Martin); Allt Tasabhaig, Applecross, rocks in gulley, NG68524806, 28 July 2017, S.V. O'Leary s.n. (E); Toscaig, Applecross, 57.37955N, 5.80155W, Steinblock im Bach, Spritzzone, 30m, NG716385, 27 July 2017, T. Kiebacher (BBSUK; Herb. Kiebacher); Applecross River, lower reaches, shaded rocks by stream, 20m, NG7145, 23 July 2017, D.F. Chamberlain s.n. (E: 00797144); S. bank of Allt na h-Airighe Riabhaich, rocks in river, 225m, NG75415035, 27 Jule 2017, E.M. Kungu (E); Tollie Bay, NW end of Loch Maree, stones in burn in NE-facing woodland, 25m, NG872777, 31 July 1986, D.G. Long

13702 (E: 00844507); R. Ewe, Poolewe, rocks in river, 10m, NG8582880691, 23 July 2012, J. Forsyth & M. Nicolson (E); R. Shiel, upstream of Achnangart, rocks in river, NG970147, 17 September 2008, D. Hicks (E); Torridon, boulder by river, NG95, 10 September 1944, E.V. Watson s.n. (E: 00844512); Talladale River ravine, wet rocks in ravine, 80m, NG916690, 2 August 1986, D.G. Long 13757 (E: 00844506); Gleann Airigh Chomhaich, S of Loch Maree, on wet boulder by stream, 65m, NG92806935, 4 October 2013, D.G. Long & J. Smith 42798 (E: 00687856); Gruinard, Poll na Fiaraich, rocks in river, 60m, NG9779388711, 17 June 2011, J. McDonald & M. Nicolson (E); Ullapool River, at footbridge in Ullapool, rocks in river, 5m, NH1265394483, 20 September 2017, J. McDonald & H. Ferguson (E); Corrieshalloch Gorge, Braemore, rocks in stream, NH27, 6 September 1960, E.F. Warburg s.n. (E: 00844501); Corrieshalloch Gorge, Ullapool, rocks in and by river, NH205780, 1 July 1966, H.J.B. Birks s.n. (E: 00434354).

West Sutherland (v-c 108): Creag an Spardain, Assynt, wet rocks in wooded ravine, 15m, NC221327, 23 April 1992, G.P. Rothero 92/033 (Herb. Rothero); R. Naver, 1.2km u/s Syre, rocks in river, with *H. eugyrium*, 55m, NC6902242811, 15 July 2009, M. Hauxwell (E).

Appendix 2. Specimens of *Hygrohypnum subeugyrium* from the Sino-Himalayan region

China: Yunnan: Fugong County: Gaoligong Shan, North Fork Yamu River below Shibali, rock slab by waterfall, 2510m, 27°09'56.1"N, 98°46'51.4"E, 4 August 2005, D.G. Long 34331 (E: 00425894); Fugong County: Gaoligong Shan, N Fork Yamu River above Shibali, boulder in stream, 2715m, 27°10'29.7"N, 98°45'23.3"E, 15 August 2005, D.G. Long 34811 (E); Fugong County: Burma/Yunnan border ridge near Twin Lakes, Yaping Pass, wet rocks in stream, 3613m, 27°12'03.1"N, 98°41'40.8"E, 16 August 2005, D.G. Long 34897 (E); Fugong County: Gaoligong Shan, N Fork Yamu River, W of Shibali, large boulder on river bank, 2575m, 27°10'01.2"N, 98°46'24.7"E, 18 August 2005, D.G. Long 35014 (E); Fugong County: Gaoligong Shan, Yaping Pass road above Shibali, granitic boulders in river, 2675m, 27°10'31.2"N, 98°45'25.2"E, 3 May 2004, J. Shevock 25337 (E: 00687593); Fugong County: Yaping Pass road above Shibali, granitic rock slab in rivulet, 3000m, 27°10'48.0"N, 98°43'32.9"E, 4 May 2004, J. Shevock 25384 (E); Fugong County: N Fork Yamu river above Shibali, wet boulders in splash zone, 2750m, 27°10'33.6"N, 98°45'18.1"E, 6 October 2007, J. Shevock 31092 (E); Gongshan County: Dulong Xiang, Qiqi trail between San Dui and Xishaofang, wet rock slab in stream, 2979m, 27°42'16.8"N, 98°26'02.9"E, 1 November 2004, D.G. Long 33816 (E); Gongshan County: Dulong Xiang, Qiqi trail above Dengxiaofang, wet boulder in stream, 3550m, 27°41'42.0"N, 98°27'23.4"E, 27 September 2007, D.G. Long 37167 (E); Gongshan County: above Dulong road, fork of Pula He above Daladi site, granitic boulders seasonally submerged, 3140m, 27°48'34.7"N, 98°29'53.1"E, 1 October 2002, J. Shevock 23273 (E); Gongshan County: QiQi trail above No. 12 Bridge, granitic boulders seasonally submerged, 2820m, 27°42'46.4"N, 98°30'06.3"E, 28 September 2007, J. Shevock 30900 (E).

India: Sikkim: valley at Lam Pokhari Rest House, Prek Chhu valley, wet dripping rocks in cascade, 4090m, 27° 29'N, 88° 12'E, 19 July 1992, D.G. Long 22700 (E: 00425934).

Captions for Figures

Fig. 1. *Hygrohypnum subeugyrium* (Renauld & Cardot) Broth. (A) Shoot with sporophyte, dry. (B) Habit of gametophyte, dry. (C) Stem cross section. (D) Capsule, dry. (E) Stem leaves, ventral view, wet. (F) Stem leaf apices. (G) Alar cells of stem leaves. (H) Mid-leaf cells of stem leaf. Scale bars: (A) = 5 mm; (B) = 2 mm; (C, F-H) = 50 µm; (D) = 1 mm; (E) 0.5 mm. All from *T. Kiebacher 1519*.

Fig.2 Leaf base and stem section of *Hygrohypnum subeugyrium*. (A) bulging row of alar cells, (B) stem cortex with thick-walled outer cells.

Fig.3 Leaf base and stem section of *Hygrohypnum eugyrium*. (A) isodiametric group of large inflated alar cells, (B) weakly differentiated stem cortex with thin outer walls, (C) stem cortex with outer walls tending to collapse inwards, (D) alar cells in section.

Fig. 4. Distribution of *Hygrohypnum subeugyrium* in Britain as currently known.